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Marine Reptiles from the Triassic of the Tre Venezie Area, Northeastern Italy

Olivier Rieppel
Fabio Marco Dalla Vecchia

JAN 10 2002

January 31, 2001
Publication 1511

PUBLISHED BY FIELD MUSEUM OF NATURAL HISTORY

JAN 18 2002

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Marine Reptiles from the Triassic of the Tre Venezie Area, Northeastern Italy

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Accepted March 15, 1999
Published January 31, 2001
Publication 1511

PUBLISHED BY FIELD MUSEUM OF NATURAL HISTORY

© 2001 Field Museum of Natural History
ISSN 0096-2651
PRINTED IN THE UNITED STATES OF AMERICA

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Marine Reptiles from the Triassic of the Tre Venezie Area, Northeastern Italy

Olivier Rieppel **Fabio Marco Dalla Vecchia**

Abstract

Ichthyosaurian and sauropterygian remains are described from Triassic deposits in the Tre Venezie area of northeastern Italy. The taxa recorded include *Mixosaurus, Cymbospondylus,* ?*Shastasaurus, Placodus,* ?*Cyamodus,* an as yet unnamed cyamodontoid placodont, *Nothosaurus* sp., and *Nothosaurus* cf. *N. giganteus.* The temporal distribution of these fossils ranges from the earliest Anisian to the middle Carnian. *Placodus* (from the lower upper Anisian Calcare di Recoaro Formation of Vallarsa and Recoaro) is recorded for the first time (on the basis of diagnostic material) from the Alpine facies of the Middle Triassic. Collectively, the sauropterygian fauna from the Tre Venezie area resembles that of the eastern Alpine Triassic more closely than that of the southwestern Alps. This may indicate two separate colonization events of the Alpine Triassic as intraplatform basins developed along the northwestern Tethyan margin.

Introduction

A number of taxa of marine reptiles (Thalattosauria, Ichthyosauria, and Sauropterygia) have been collected over the years from Triassic deposits in the Tre Venezie area of northeastern Italy (Trentino–Alto Adige, Veneto, and Friuli–Venezia Giulia). The localities yielding Paleozoic and Mesozoic reptiles in these areas have been catalogued by Sirna et al. (1994), along with an identification of the faunal elements found at the respective localities (Fig. 1). Some of the material has been described in greater detail, such as thalattosaur caudal vertebrae, nothosaur ("*Paranothosaurus*") vertebrae, and a tooth-bearing palatine fragment of a cyamodontoid placodont (Dalla Vecchia, 1993). Other material has remained undescribed and forms the basis of the present study.

The occurrences of Sauropterygia and other marine reptiles in the Alpine Triassic range from the early Anisian (Sirna et al., 1994; Rieppel & Hagdorn, 1997) to the Rhaetian (Pinna, 1990). Lower Anisian records are exceedingly rare, not so much because of a sampling bias, but rather because the characteristic intraplatform basin habitats did not develop along the southeastern shelf of the European platform before the late Anisian. It is at the Anisian–Ladinian boundary that the fossil record of marine reptiles becomes richer in the Alpine Triassic. A well-corroborated phylogeny on which paleobiogeographic reconstructions can be based is available for the Sauropterygia only at this time (Rieppel, 1999a). Given the paleobiogeographic reconstruction of the late Anisian western Tethyan realm by Marcoux et al. (1993) and the phylogenetic relationships of the Sauropterygia (Rieppel, 1997, 1998a), alternative scenarios can be reconstructed for the invasion of the Alpine Triassic by Sauropterygia. A detailed comparison of the faunas from the Germanic Triassic (Muschelkalk) and from the southern Alps (Monte San Giorgio and equivalent deposits in northern Italy; Perledo) led Rieppel and Hagdorn (1997) to conclude that sauropterygians invaded the southern Alpine realm through a southern gateway (Burgundian Gate), which linked the Anglo-Germanic Basin with the developing southern branch of the Neotethys. In view of their eastern affinities (with Chinese taxa such as *Sanchiaosaurus, Keichousaurus,* and *Hanosaurus:* Rieppel & Lin, 1995; Rieppel, 1998a, 1999b), sauropterygians might alternatively have reached the eastern

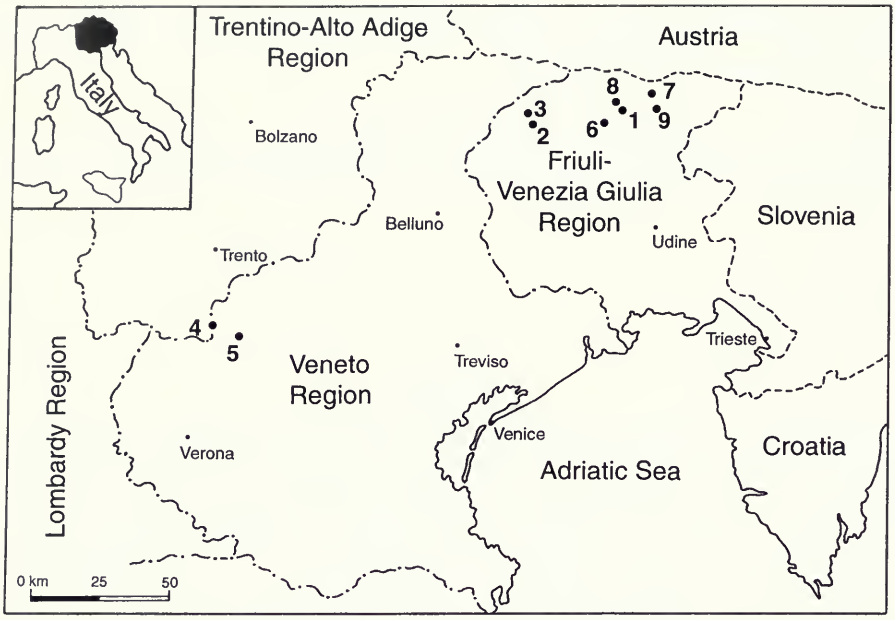


FIG. 1. Localities in the Tre Venezie area (NE Italy) yielding Triassic marine vertebrates. **1,** Ambruseit Creek, Arta Terme (Udine Province); **2,** Clap di Val, Forni di Sotto (Udine Province); **3,** Pian delle Streghe locality of Bivera Mountain, Forni di Sotto (Udine Province); **4,** Leno Creek, Specchieri (Trento Province); **5,** Recoaro, (Vicenza Province); **6,** Fusea near Tolmezzo (Udine Province); **7,** Fus Creek, Moggio Udinese (Udine Province); **8,** Mt. Tersadia, Arta Terme (Udine Province); **9,** Lavaz Creek, Dogna (Udine Province).

Alpine realm along the southeastern continental shelf of Europe, bordering on the western Tethys in the northeast and on the western branch of the Neotethys in the south. In view of these alternative scenarios, a more detailed analysis of marine reptiles from the Triassic of the southeastern Alps is likely to provide important new information on the paleobiogeography of this region.

Systematic Paleontology

Ichthyosauria Blainville, 1835
Mixosauridae Baur, 1887
***Mixosaurus* Baur, 1887**

***Mixosaurus* sp.**

MATERIAL—Museo Friulano di Storia Naturale (MFSN), Udine, no. 19385; a partially disarticulated string of 15 caudal vertebral centra (of which 3 are poorly preserved) associated with neural arches (Fig. 2).

LOCALITY AND HORIZON—Ambruseit Creek, Arta Terme, Province of Udine, Friuli–Venezia Giulia Region. Lower Pelsonian (*Cuccense* subzone), lowermost upper Anisian.

The specimen (MFSN 19385) was collected by C. Rosenfeld in the bed of Ambruseit Creek near the village of Piedim (Arta Terme). Specimen MFSN 19385 comes from alternating black siltstones and gray nodular limestones with subordered black marly limestones. This interval is situated below and in continuity with the Bivera Formation (lower Illyrian; Farabegoli et al., 1984) and is attributed to the Dont Formation (Carulli et al., 1987). On the basis of ammonoids, the age can be determined as early Pelsonian, earliest late Anisian (P. Mietto, pers. comm.).

The specimen comprises a total of 15 caudal vertebral centra, of which 3 are very incompletely preserved (Fig. 2). All vertebral centra are weathered to a sagittal or parasagittal plane, exposing their deeply amphicoelous and notochordal structure. The length of the centra ranges from 12.5 to 6 mm, and their height varies from 15 to 14 mm; the height/length ratio varies from 1.12 to 2.3. Associated with the caudal centra are neural arches carrying tall neural spines. The basal portions of the neural arches are sutured but not fused to the vertebral centra. The bases (pedicels) of the neural

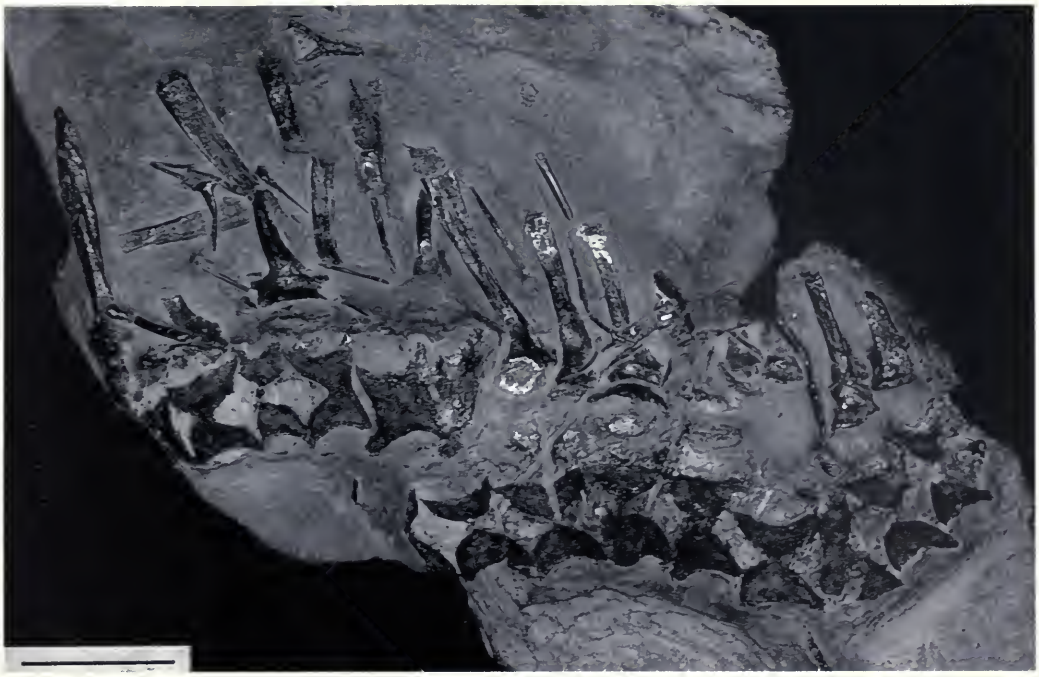


FIG. 2. *Mixosaurus* sp. (MFSN 19385) from Arta Terme, Ambruseit Creek, Province of Udine, lowermost upper Anisian. Scale bar = 20 mm.

arches are generally expanded; one well-preserved and complete neural arch is remarkable in that it shows a greatly expanded pedicel, which appears to carry distinct pre- and postzygapophyses (Fig. 3). Repossi (1902, pl. IX, fig. 9e) figured the neural arches of tail vertebrae of *Mixosaurus cornalianus,* which bear pre- and postzygapophyses but show much less expanded pedicels. The neural spines are slender and elongate. They slant slightly posterodorsally and show a slight curvature, resulting in a concave anterior and convex posterior margin. Elongation and curvature of the neural spines are characteristic of the middle tail section of *Mixosaurus* (Repossi, 1902). Only a single element is preserved that can be identified as an incomplete chevron.

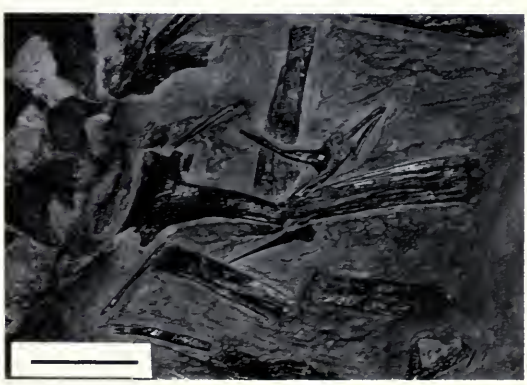


FIG. 3. Neural arch of *Mixosaurus* sp. (MFSN 19385). Scale bar = 10 mm.

Mixosaurus has a cosmopolitan distribution during the Middle Triassic (Callaway & Massare, 1989; Mazin & Sander, 1993; Sander & Mazin, 1993), with five species currently recognized. These are *Mixosaurus atavus* (Quenstedt, 1852), from the lower Muschelkalk of southern Germany; *Mixosaurus cornalianus* (Bassani, 1886), from the *Grenzbitumen* horizon (Anisian–Ladinian boundary) of southern Switzerland and northern Italy; *Mixosaurus nordenskioeldii* (Hulke, 1873), from the Middle Triassic of Spitzbergen and British Columbia; *Mixosaurus natans* (Merriam, 1908), from the Middle Triassic of northwestern Nevada (Sander & Bucher, 1990); and *Mixosaurus maotaiensis* Young, 1965, from the lower Middle Triassic of China (Kweichou Province). Early Triassic remains of *Mixosaurus* have been reported from British Columbia (Callaway & Brinkman, 1989), while in the Anglo-Germanic Basin, *Mixosaurus* extends back to the Gogolin beds (?Bithynian, lower Anisian) of Gorny Slask (Huene, 1916). Coming from the Pelsonian (low-

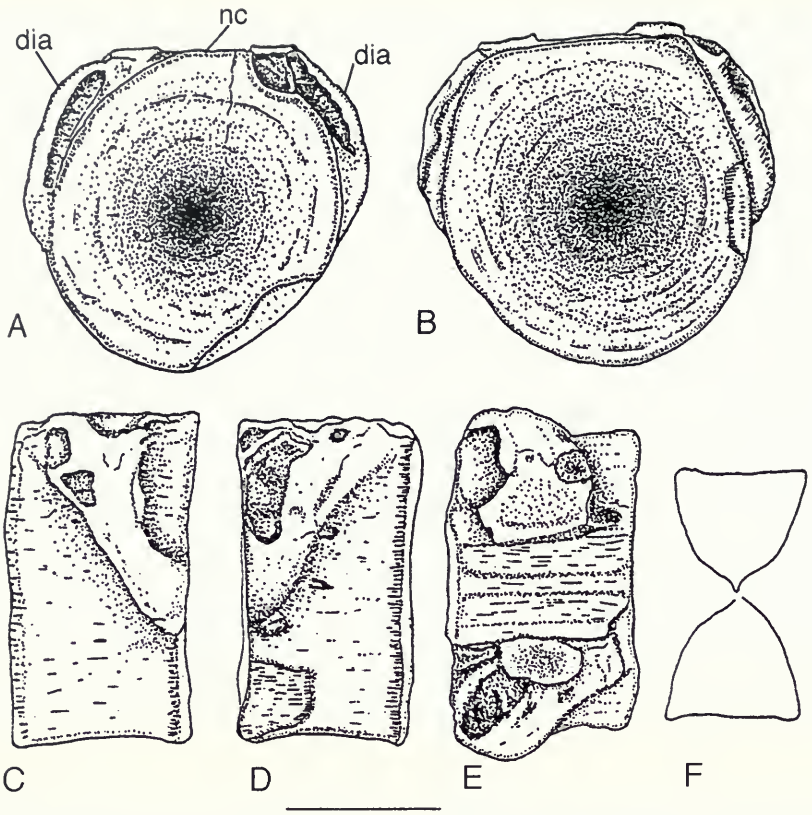


FIG. 4. ?*Cymbospondylus* sp. (MFSN 15275); isolated dorsal vertebral centrum from Clap di Val, Forni di Sotto, Province of Udine, upper Ladinian. **A,** Anterior view; **B,** posterior view; **C,** right lateral view; **D,** left lateral view; **E,** dorsal view; **F,** cross-sectional area. Scale bar = 20 mm. Abbreviations: dia, diapophysis (for the rib articulation); nc, neural canal.

ermost upper Anisian), the specimen MFSN 19385, from the Carnian Alps, is the earliest record for the genus in the Alpine Triassic. The incompleteness of the fossil renders comparison with other species of *Mixosaurus* difficult, but the broad expansion of the pedicel of the neural arch appears to be a unique character of the Friulian specimen.

Shastasauridae Merriam, 1902
Cymbospondylus Leidy, 1868

?*Cymbospondylus* sp.

MATERIAL—Museo Friulano di Storia Naturale, Udine, no. 15275; isolated dorsal vertebral centrum. Museo Paleontologico of Portogruaro (Venezia), uncatalogued specimen; isolated dorsal vertebral centrum.

LOCALITY AND HORIZON—Clap di Val, Forni di Sotto, Province of Udine. "Formazione delle calcareniti rosse e grigie," Longobardian, upper Ladinian.

The vertebrae were collected at the locality of Clap di Val, near the village of Forni di Sotto (Udine). Specimen MFSN 15275 comes from the UA5 interval of "red and gray calcarenites Formation" (Pisa, 1966), dated to as early as middle Longobardian (late Ladinian: P. Mietto, pers. comm.), from which a rich ammonoid fauna was collected as well. It is a nearly complete centrum, lacking only a small splinter in the ventrolateral anterior part (Fig. 4). In posterior view it is slightly deformed by lithostatic pressure. It is 23.6 mm long, 42.8 mm high (1.81 height/length ratio), and the horizontal diameter is 46.0 mm (anterior surface) and 39.5 mm (posterior surface), respectively. The anterior and posterior ends of the centrum are deeply amphicoelous and notochordal, but the articular surface is only weakly inclined in the

FIG. 5. ?*Cymbospondylus* sp. (MFSN 15275); isolated dorsal vertebral centrum in right lateral view. Scale bar = 20 mm.

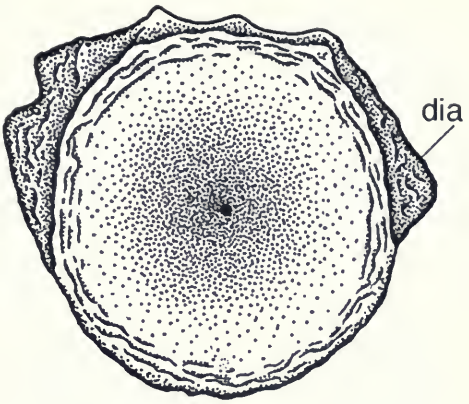


FIG. 6. ?*Cymbospondylus* sp. (Museo Paleontologico of Portogruaro, uncatalogued); isolated dorsal vertebral centrum from Clap di Val, Forni di Sotto, Province of Udine, upper Ladinian, in anterior view. Scale bar = 10 mm. Abbreviation: dia, diapophysis (for the rib articulation).

peripheral part, becoming steeper in the central part. The body of the centrum is constricted. The elongated diapophysis is located high on the centrum, and, as it descends in an anterior curve along the side of the centrum, it appears truncated at the anterior margin of the centrum (Fig. 5). This pattern of rib articulation is typical for anterior and middle dorsal vertebrae of *Cymbospondylus* (Sander, 1997), although McGowan (1994) questions the reliability of this character for the identification of isolated ichthyosaur vertebrae.

The uncatalogued specimen from the Museo Paleontologico of Portogruaro (Venezia) comes from an unknown level of the same section and is a nearly complete centrum (Fig. 6). It is slightly eroded along its anterior and posterior margins but not deformed. It is 20 mm long, 43.8 mm high, and 48 mm wide. It is deeply amphicoelous, perhaps notochordal, and its transverse outline is subhexagonal, with a more pronounced flat dorsal surface forming the floor of the neural canal. The anterior and posterior articular surfaces are regularly concave from the periphery to the center of the centrum, showing an hourglass shape in anteroposterior section. The articular facets for the neural arch are well developed and slightly wider than the neural canal, which is 8–9 mm wide at the margins of the centrum. The diapophysis extends diagonally from the middle-upper part of the lateral side of the centrum to the middle of the anterior margin; a ridge reaches the middle of the dorsal margin of the centrum, and its dorsal termination is in contact with the articular facet of the neural arch. The anteroventral end of the diaphysis is confluent with the anterior side of the centrum and appears to be truncated by it. There is no trace of a parapophysis.

Cymbospondylus is a widely distributed ichthyosaurian genus during the Middle Triassic (Sander, 1992; Mazin & Sander, 1993; Sander & Mazin, 1993), with two previous records from the Alpine Triassic: one in the *Grenzbitumen* horizon (Anisian–Ladinian) of Monte San Giorgio and the other from the Buchensteiner beds (Ladinian) of Mt. Seceda (Province of Bolzano/Bozen, northeastern Italy) (Sander, 1989).

?*Cymbospondylus* sp.

MATERIAL—Museo Friulano di Storia Naturale, Udine, nos. 19389, 19390; isolated posterior dorsal vertebral centra, associated with a neural spine (MFSN 19388), the proximal part of a rib (MFSN 19387), and two rib fragments (MFSN uncatalogued).

LOCALITY AND HORIZON—Pian delle Streghe locality of Bivera Mountain, Forni di Sotto, Prov-

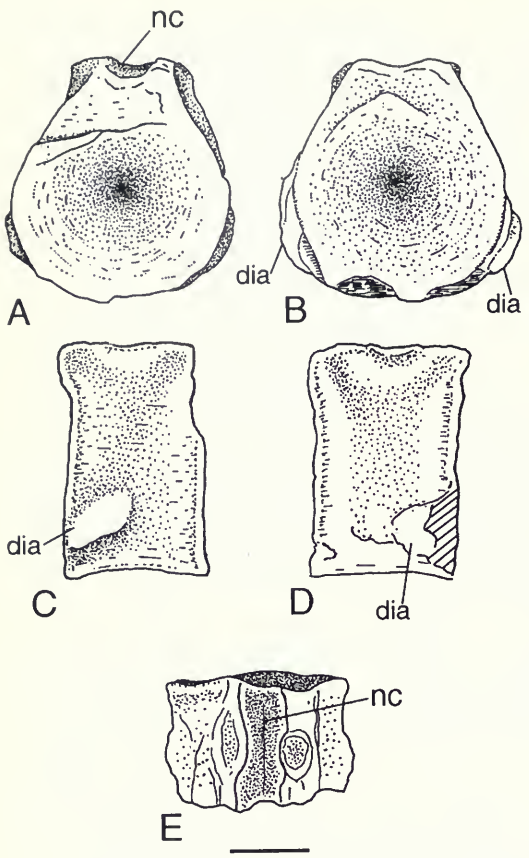


FIG. 7. ?*Cymbospondylus* sp. (MFSN 19390); isolated dorsal vertebral centrum from the Pian delle Streghe locality, Forni di Sotto, Province of Udine, lower upper Anisian. **A,** Posterior view; **B,** anterior view; **C,** left lateral view; **D,** right lateral view; **E,** dorsal view. Scale bar = 10 mm. Abbreviations: dia, diapophysis (for the rib articulation); nc, neural canal.

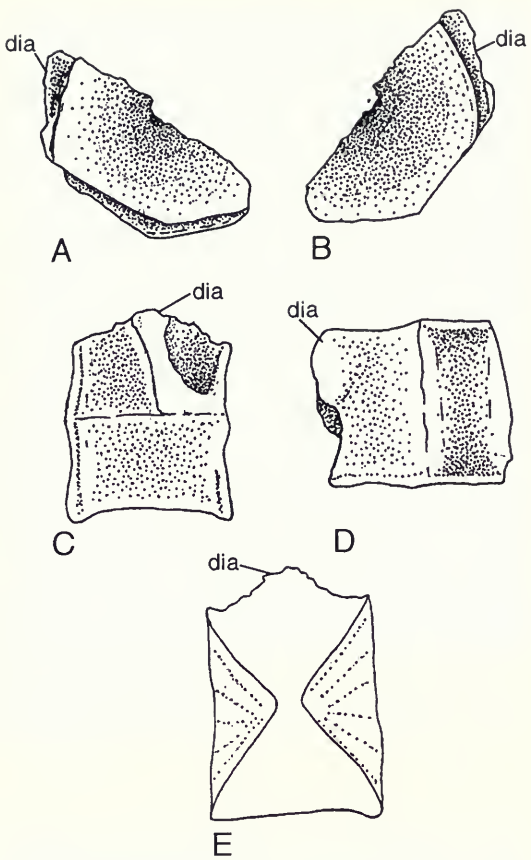


FIG. 8. ?*Cymbospondylus* sp. (MFSN 19389); partial dorsal vertebral centrum from the Pian delle Streghe locality, Forni di Sotto, Province of Udine, lower upper Anisian. **A,** Anterior view; **B,** posterior view; **C,** right lateral view; **D,** ventral view; **E,** cross-sectional area. Scale bar = 10 mm.

ince of Udine. Dont Formation, *Balatonicus* subzone, Pelsonian, lower upper Anisian.

The nearly complete centrum (MFSN 19390, Fig. 7) was collected by Mr. A. Tarlao at the Pian delle Streghe locality at the base of the northeastern slope of Mt. Bivera. It was found in an isolated block, but the lithology indicates its provenance from the outcrop just above the block, and a rich fauna of silicified small ammonoids permits its attribution to the Dont Formation (Pelsonian, lower upper Anisian). The ammonoids indicate a slightly younger age than for the *Mixosaurus* specimen described above (P. Mietto, pers. comm.).

The deeply amphicoelous and notochordal centrum is 19.5 mm long, the vertical diameter is 33.5 mm, and the maximal horizontal diameter is 32.5 mm. The cross section of the centrum resembles a dorsally truncated triangle. It is narrow dorsally, the well-defined neural canal forming a distinct notch in its dorsal margin. It is wider and evenly rounded ventrally. The diapophysis is small, ovoid, and obliquely elongated; it is situated anteroventrally on the lateral aspect of the centrum, truncated anteriorly by the anterior margin of the centrum. This vertebral structure is characteristic of posterior dorsal vertebrae of *Cymbospondylus* (Merriam, 1908).

Along with the centrum MFSN 19390, the block yielded half of a second vertebral centrum (MFSN 19389, Fig. 8), an isolated neural spine (MFSN 19388, Fig. 9 A–C), and the proximal part of a rib (MFSN 19387, Fig. 9D–E), as well as two rib fragments. These bones were not in articulation, but were preserved in association and probably

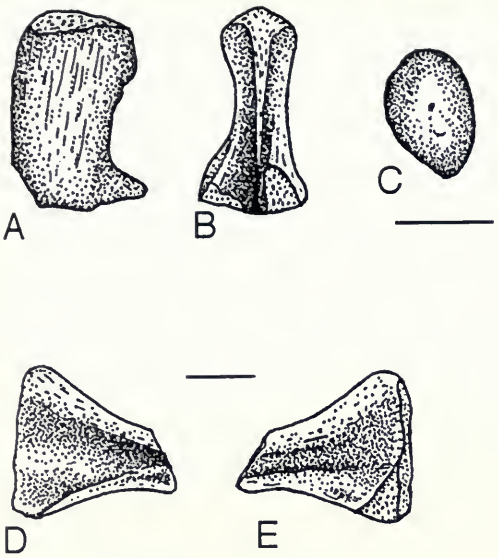


FIG. 9. **A–C:** ?*Cymbospondylus* sp. (MFSN 19388); isolated neural arch from the Pian delle Streghe locality, Forni di Sotto, Province of Udine, lower upper Anisian. **A,** Left lateral view; **B,** posterior view; **C,** dorsal view. Scale bar = 10 mm. **D–E:** ?*Cymbospondylus* sp. (MFSN 19387); proximal head of a rib from the Forni di Sotto, Pian delle Streghe locality, Province of Udine, lower upper Anisian. **D,** Anterior view; **E,** posterior view. Scale bar = 10 mm.

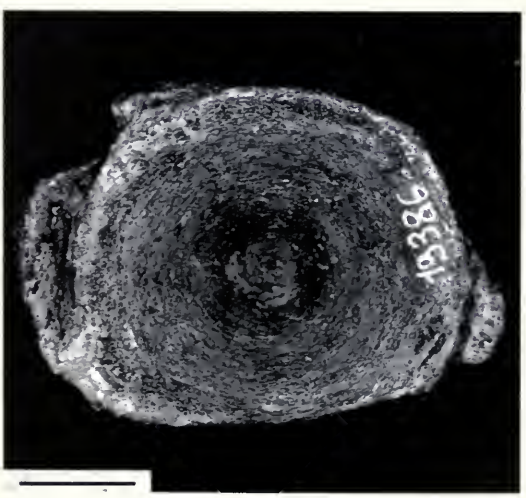


FIG. 10. ?*Shastasaurus* sp. (MFSN 19386); isolated dorsal vertebral centrum from the Pian delle Streghe locality, Forni di Sotto, Province of Udine, upper Anisian, in anterior view. Scale bar = 10 mm.

belong to the same individual. The specimen MFSN 19389 is the ventral half of a centrum, representing most of the ventral and right lateral sides. The height of the preserved portion is 27 mm; the length is 23.2 mm. The preserved part indicates a hexagonal circumference of the centrum. It is deeply amphicoelous, but a notochordal perforation cannot be identified. The ventral face shows a shallow longitudinal depression in its middle part. The diapophysis is L-shaped and anteriorly truncated, as is typical of posterior dorsal vertebrae of *Cymbospondylus* (Merriam, 1908).

The neural spine (MFSN 19388) is very short, claviform, and expanded at the apex. The proximal part of the rib (MFSN 19387) is single-headed, triangular, and much expanded; the proximal shaft is rather narrow.

Being of Pelsonian age, these remains are likely to be the earliest record of *Cymbospondylus* in the Alpine Triassic (see above for caveats regarding identification of isolated shastasauriform vertebrae). In the Anglo-Germanic Basin, shastasauriform ichthyosaurs appear only in the upper Muschelkalk (upper Illyrian, upper Anisian: Huene, 1916; Sander, 1997).

Shastasaurus Merriam, 1895

?*Shastasaurus* sp.

MATERIAL—Museo Friulano di Storia Naturale, Udine, no. 19386; isolated dorsal vertebral centrum (Fig. 10).

LOCALITY AND HORIZON—Pian delle Streghe locality of Bivera Mountain, Forni di Sotto, Province of Udine. Bivera Formation, lower Illyrian, upper Anisian.

The specimen was collected by C. Calligaris at the Pian delle Streghe locality at the base of the northeastern slope of Bivera Mountain (Udine). It comes from the Bivera Formation (lower Illyrian, upper Anisian: Farabegoli et al., 1984), which overlies the Dont Formation, where the remains described above were found.

The deeply amphicoelous and notochordal centrum (MFSN 19386, Fig. 10) was originally preserved in a pink-reddish limestone, with the dorsal and ventral sides weathered. As a result, the articular facets of the neural arch, as well as the ventral curvature, are not preserved. The centrum is 19.4 mm long, its vertical diameter is 29.7 mm (incomplete), and its horizontal diameter is 44.7 mm (measured across the anterior surface). The right rib articulation is a knob-like protuberance

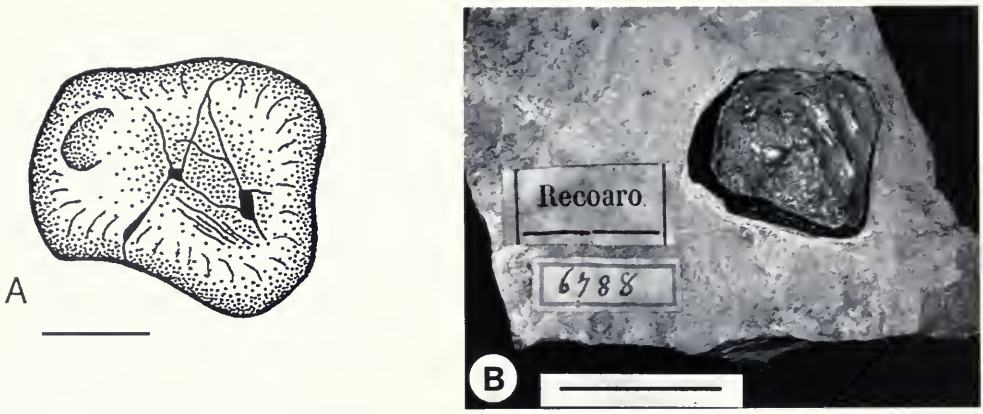


FIG. 11. **A,** *Placodus* cf. *P. gigas* (Museo Tridentino di Scienze Naturali, Trento, uncatalogued); posterior palatine tooth plate from Specchieri, Leno Creek, Vallarsa, Trento Province, lower upper Anisian. Scale bar = 5 mm. **B,** *Placodus* cf. *P. gigas* (University of Padua Museum of Paleontology, no. 6788); posterior palatine tooth plate from Recoaro, Province of Vicenza, Veneto Region, lower upper Anisian. Scale bar = 20 mm.

located low on the lateral surface of the centrum. It appears to be incomplete by comparison to the left diapophysis, which is an elongated and curved structure typical for shastasaurids. The ventral extension of the diapophysis remains well separated from the anterior margin of the centrum, corresponding to the condition observed in dorsal vertebrae of *Shastasaurus* (Merriam, 1902) rather than that of *Cymbospondylus* (Sander, 1997).

Although the rib articulation may not be sufficient grounds on which to identify genera of shastasauriform ichthyosaurs, an anteriorly curving diapophysis is present in *Cymbospondylus* (Merriam, 1908), but absent in all other representatives of this clade. The latter include the genera *Shastasaurus* Merriam, 1895, and *Shonisaurus* Camp, 1976. Of these, *Shastasaurus* is known from the Germanic Muschelkalk (upper Anisian: Sander, 1997) and from the upper Ladinian (or Carnian) of the eastern Alps (Huene, 1925; see also McGowan, 1994). If specimen MFSN 19386 is referable to *Shastasaurus,* it would be the earliest record of that genus in the Alpine Triassic.

Sauropterygia Owen, 1860
Placodontia Cope, 1871
Placodontoidea Cope, 1871
Placodontidae Cope, 1871
***Placodus* Agassiz, 1833–1845**

Placodus* cf. *P. gigas

MATERIAL—Museo Tridentino di Scienze Naturali, Trento, uncatalogued; an isolated palatine tooth plate of *Placodus* cf. *P. gigas* (Fig. 11A).

LOCALITY AND HORIZON—Specchieri, Leno Creek, Vallarsa, Trento Province, Trentino–Alto Adige Region. Calcare di Recoaro (Recoaro Limestone) Formation, Pelsonian, lower upper Anisian.

The specimen is a slightly crushed but otherwise well-preserved palatine tooth plate of *Placodus* (Fig. 11A). It has an irregular rectangular outline with a slightly concave anterior and a slightly convex posterior margin. This shape is characteristic of the second palatine tooth plate in *Placodus gigas* (Rieppel, 1995a). The maximal longitudinal diameter of the tooth plate is 12.5 mm; its transverse diameter is 14 mm.

The specimen reported here is the earliest record for *Placodus* in the Alpine Triassic; the earliest appearance of *Placodus* in the Anglo-Germanic Basin is in the Gogolin beds of Gorny Slask, which are very closely comparable to the *Gracilis* Formation (Bithynian) of northeastern Italy (H. Hagdorn, pers. comm.).

Placodus* cf. *P. gigas

MATERIAL—University of Padua Museum of Paleontology, no. 6788: an isolated palatine tooth plate (Fig. 11B).

LOCALITY AND HORIZON—Recoaro, Province of Vicenza, Veneto Region. Calcare di Recoaro (Recoaro Limestone), Pelsonian, lower upper Anisian.

The tooth crown shows roughly square contours, with a longitudinal diameter of 21.1 mm and a transverse diameter of 23.2 mm (Fig. 11B).

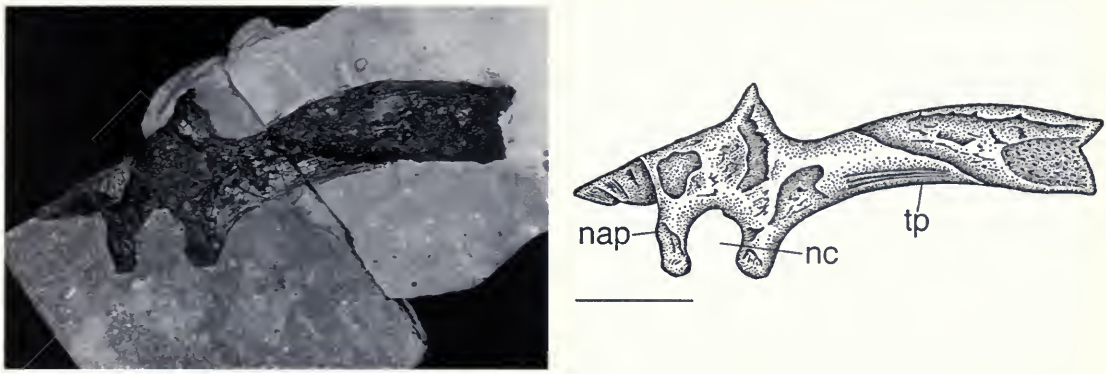


FIG. 12. *Cyamodontoidea* indet. (MFSN 15698); incomplete neural arch from Fusea near Tolmezzo, Province of Udine, middle Carnian. Scale bar = 20 mm. Abbreviations: nap, neural arch pedicel; nc, neural canal; tp, transverse process.

Its size and shape are characteristic of the posterior palatine tooth plate of *Placodus* (Rieppel, 1995a).

The genus *Placodus* is well represented from the early Anisian (lower Muschelkalk) through the early Ladinian (upper Muschelkalk) of the Germanic Triassic. The genus has also been reported from the Anisian of Transylvania, Rumania ("*Placodus gracilis*": Jurcsak, 1976), and from the late Anisian and early Ladinian of Israel (Haas, 1975), but whereas cyamodontoid placodonts are well known from both these latter localities, none of the material is diagnostic for the genus *Placodus*. Placodont remains have been reported (but not described) from the Anisian and early Ladinian of the eastern Alps (Furrer et al., 1992), and without reference to diagnostic characters one tooth was listed as *Placodus* sp. by Bürgin et al. (1991: Table 4). This latter tooth is "small," with an elliptical cross section, and might just as well represent a cyamodontoid (H. Furrer, in litt., 6 November 1997). The isolated yet diagnostic teeth from Leno Creek (Trento Province) and from Recoaro for the first time unequivocally demonstrate the occurrence of the genus *Placodus* outside the Anglo-Germanic Basin. The isolated occurrence of this genus in the lower upper Anisian of the southeastern Alps only is intriguing in view of the fact that thousands of vertebrate fossils have been collected from the southern Alpine Grenzbitumen horizon (Anisian–Ladinian boundary) at Monte San Giorgio or from equivalent beds in northern Italy, with not a single record of that genus.

Cyamodontoidea Nopcsa, 1923

Cyamodontoidea indet.

MATERIAL—Museo Friulano di Storia Naturale, Udine, no. 15698, incomplete neural arch (Fig. 12).

LOCALITY AND HORIZON—Fusea near Tolmezzo, Province of Udine. "Black limestones" just above the "Dolomia Cassiana 2" (De Zanche et al., 1993), uppermost Julian, middle Carnian.

The dolostone lithosoma in the area of Fusea was identified as "Dolomia dello Schlern" in the geological map of that area (Braga et al., 1971). However, its position just below the Raibl Group indicates that it is the last Carnian carbonate platform, that is, that it corresponds to the "Dolomia Cassiana 2" (*sensu* De Zanche et al., 1993), known also as Upper Cassian Dolomite ("Dolomia Cassiana Superiore").

The specimen is a partially preserved, much weathered neural arch with a massive, elongate transverse process, as is diagnostic of the dorsal vertebrae of cyamodontoid placodonts (Fig. 12). As preserved, the total width of the specimen is 94.1 mm and its maximum height is 34.5 mm. The distinct pedicels of the neural arch define the neural canal, which is 9.6 mm wide and 14.0 mm high. Weathering has obscured all details of the intervertebral articulation. Comparable dorsal neural arches are known for *Cyamodus* (Pinna, 1992; Rieppel, 1995b, Fig. 4), whereas those of *Psephoderma* show a distinct proximal constriction of the transverse processes (Pinna & Nosotti, 1989).

A skull and other placodont remains from the same horizon and locality have been described and identified as *Placochelys placodonta* (Pinna & Zucchi Stolfa, 1979; see also Zucchi Stolfa, 1975). The skull, which is now lost, was badly crushed and lacked the rostrum. It showed few structural details beyond the dentition and the general contours of the posterior part of the skull, and it resembled *Cyamodus* more than *Placochelys*. The tubercular osteoderms on the posteriorly projecting squamosals are much more prominently developed in *Placochelys* than was the case in the skull from Fusea (Pinna & Zucchi Stolfa, 1979, Pl. 13). In fact, the incompleteness of the material renders its generic identification questionable. Pinna and Zucchi Stolfa (1979) may have identified the placodont from Fusea as *Placochelys* because they considered the outcrops at the latter locality to be of equivalent age as the Hungarian deposits that have yielded *Placochelys*. The carapace fragments from the Fusea locality, however, are strikingly different from those of *Placochelys* (Jaekel, 1907). They most likely represent the same taxon as the skull described by Pinna and Zucchi Stolfa (1979), and strongly suggest that the cyamodontoid from northeastern Italy was not congeneric with *Placochelys*.

Cyamodontoidea indet.

MATERIAL—Museo Friulano di Storia Naturale, Udine, nos. 15700, 19178, 22751, and 22760–22763; carapace fragments. MFSN 22759; complete carapace.

LOCALITY AND HORIZON—Fusea near Tolmezzo, Province of Udine. "Black limestones" just above the "Dolomia Cassiana 2" (De Zanche et al., 1993), uppermost Julian, middle Carnian.

Several carapace fragments (Fig. 13A–B), as well as one completely preserved, still incompletely prepared carapace, indicate a unique type of osteoderm arrangement, which suggests the presence, at Fusea, of a new taxon of cyamodontoid placodont.

The contours of the carapace are oblong, with a distinctly concave nuchal region (Fig. 14). The dorsolateral margins of the carapace are strengthened by enlarged tubercles (not present in the nuchal region) with an irregularly polygonal (octagonal to hexagonal) base and a central apex. Below these marginal tubercles, the carapace descends ventrally to cover the flank of the body. Along its lateral and anterior margins, the carapace is distinctly thickened in cross section, but it becomes progressively thinner toward the dorsal midline of the body.

In addition to the two marginal rows of enlarged tubercles, the dorsal side of the carapace is ornamented by three more rows of enlarged osteoscutes, a dorsomedial one and two dorsolateral ones. These rows of enlarged tubercles are flanked by smaller osteoderms of triangular shape, with a blunt apex and a rounded base. Collectively, these osteoderms form a highly characteristic "fish-scale" pattern. At increasing distance from the row of enlarged tubercles, these smaller osteoderms gradually change their shape to become rhomboid, pentagonal, or hexagonal elements.

A more detailed description of the dermal armor of the Fusea cyamodontoid must await the complete preparation and restoration of the specimen. The information already available, however, allows the conclusion that the dermal ornamentation of this carapace is fundamentally different from that of *Placochelys* (Jaekel, 1907). It is also very distinct from the carapace of *Psephoderma*, which is composed of regularly shaped hexagonal elements of subequal size and with fringed margins, resembling the Fusea cyamodontoid only by having three longitudinal rows of enlarged osteoscutes in addition to the two lateral rows fortifying the lateral margins. The carapace of *Cyamodus hildegardis* is less well known in dorsal view, but it appears to be composed of less regularly formed osteoderms and is not known to have three longitudinal ridges formed by enlarged osteoderms in addition to the thickened lateral margins.

***Cyamodus* Meyer, 1863**

?*Cyamodus* sp.

MATERIAL—Museo Friulano di Storia Naturale, Udine, no. 16848; fragmentary palatine bone (Fig. 15).

LOCALITY AND HORIZON—Fus Creek, Val Aupa, Moggio Udinese, Province of Udine. "Terrigeno Ladinico," upper Ladinian.

The specimen was previously described and figured by Dalla Vecchia (1993). It was found to closely resemble *Cyamodus hildegardis* (Peyer, 1931) from the *Grenzbitumen* horizon (Anisian–Ladinian boundary) of Monte San Giorgio. It should be noted, however, that the genus *Cyamodus* is based on material from the Germanic Tri-

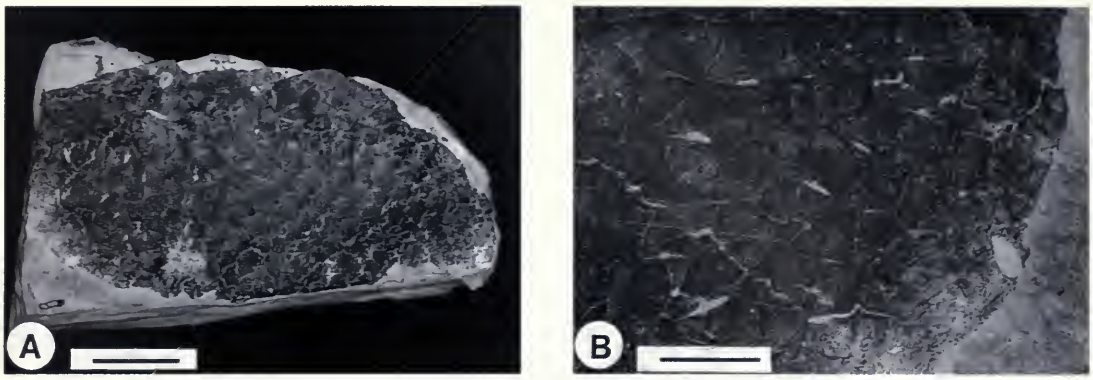


FIG. 13. Cyamodontoidea indet., carapace fragment. **A,** MFSN 15700 from Fusea near Tolmezzo, Province of Udine, middle Carnian; scale bar = 50 mm. **B,** Close-up view of the marginal area of the same specimen; scale bar = 20 mm.

assic (Meyer, 1863) and that *hildegardis* may not be congeneric with *Cyamodus* (Nosotti & Pinna, 1996). Dalla Vecchia (1993, p. 55) only tentatively referred the specimen to the genus *Cyamodus.*

Eosauropterygia Rieppel, 1994
Nothosauridae Baur, 1889
***Nothosaurus* Münster, 1834**

***Nothosaurus* sp.**

MATERIAL—Museo Friulano di Storia Naturale, Udine, no. 15611; rib fragment with isolated tooth (Fig. 16).

LOCALITY AND HORIZON—Mt. Tersadia Massif, Arta Terme; Dolomia del Serla Inferiore (Lower Serla Dolomite) Formation, Dolomia di Frassené Member, Aegean, lowermost Anisian.

The specimen consists of the proximal end of a broken dorsal rib, associated with a tooth (Fig. 16). The tooth represents an anteriorly placed fang and is approximately 15 mm long (its base is obscured by the overlying rib). The tooth crown is recurved and pointed, and the enamel covering is distinctly striated, as is characteristic for *Nothosaurus.*

Coming from the lowermost Anisian, the specimen represents the earliest record of the genus *Nothosaurus* in the Alpine Triassic.

***Nothosaurus* sp.**

MATERIAL—Museo Civico, Valdagno (Vicenza), uncatalogued; incomplete femur (Fig. 17).

LOCALITY AND HORIZON—Recoaro, Province of Vicenza, Veneto Region. Formazione a *Gracilis,* Bithynian, lower Anisian.

COMMENTS—The specimen represents the proximal part of an incomplete femur of 78 mm length. The bone is slender and slightly sigmoidally curved (Fig. 17). Its minimal width is 6.5 mm; its maximal proximal width is 17 mm. Although broken superficially, the internal trochanter can be described as having been weakly developed and separated from the shaft of the femur by a very shallow intertrochanteric fossa, as is characteristic of the femur of *Nothosaurus* (Rieppel, 1994, fig. 62A).

The *Gracilis* Formation of the southeastern Alps is very closely comparable to equivalent deposits in Gogolin, Gorny Slask (H. Hagdorn, pers. comm.), and it also marks the time of the first occurrence of sauropterygians at both these localities (Rieppel & Hagdorn, 1997). Under the assumption that the *Gracilis* Formation at Recoaro remains restricted to the Bithynian, the nothosaurs from the latter locality are just slightly younger than the specimen from the Aegean described above. Collectively, they represent the earliest occurrence of *Nothosaurus* in the Alpine Triassic. The next earliest occurrences of the genus in other parts of the Alpine Triassic are around the Anisian–Ladinian boundary in the *Grenzbitumen* horizon of Monte San Giorgio, and in the eastern Alps (Furrer et al., 1992). The Recoaro locality has yielded a neural arch, possibly referable to *Cymatosaurus,* and a poorly preserved neural arch, possibly representing a pachypleurosaur (Rieppel & Hagdorn, 1997).

FIG. 14. Cyamodontoidea indet. (MFSN 22751); nuchal region of a carapace from Fusea near Tolmezzo, Province of Udine, middle Carnian. Scale bar = 40 mm.

***Nothosaurus* sp.**

MATERIAL—Museo Friulano di Storia Naturale, Udine, no. 15329; fragment of mandible (Fig. 18).

LOCALITY AND HORIZON—Mt. Tersadia, Arta Terme, Province of Udine. Bivera Formation, lower Illyrian, upper Anisian.

The specimen MFSN 15329 consists of a broken and poorly preserved fragment of a rather small right mandibular ramus that is 108.7 mm long (as preserved). All teeth are broken, but two preserve their bases and exhibit distinct striations on the enamel surface (Fig. 18). The broken teeth show no indications of plicidentine, thus ruling out referral to ichthyosaurs. The only other marine reptiles with striated enamel are nothosaurs.

***Nothosaurus* sp.**

MATERIAL—Museo Friulano di Storia Naturale, Udine, no. 21133; fragmentary neural arch (Fig. 19).

LOCALITY AND HORIZON—Lavaz Creek, Dogna, Province of Udine. Possibly "calcari e dolomie di Loveana" with *Myophoria kefersteini,* upper Julian, middle part of Carnian.

The specimen consists of an incompletely preserved, badly rolled neural arch of a small nothosaur (Fig. 19). As preserved, its total width is 21.1 mm (measured across the transverse processes); its maximal height is 14.3 mm. The dorsal margin of the neural spine is complete and indicates its low height (9.4 mm). The pedicels of the neural arch are equally low, and define a neural canal that is 5.9 mm wide and 4.9 mm high. The postzygapophyses are eroded but still remain distinct, with their articular facets facing ventrolaterally. On the rolled specimen, the zygantrum appears as a pair of distinct pits located between the postzygapophyses, indicating that in the complete vertebra the zygantrum was internally subdivided by a vertical septum.

Previously, the latest known record of *Nothosaurus* was the occurrence of *Nothosaurus edingerae* in the Gipskeuper of the Germanic Triassic (Rieppel & Wild, 1994); incomplete nothosaur remains extend up into the upper Gipskeuper of Carnian age (H. Hagdorn, pers. comm.). Together with the nothosaurs from Fusea described below, MFSN 21133 may be the latest occurrence of *Nothosaurus* in the Alpine Triassic, and it might be younger than the latest *Nothosaurus* in the Gipskeuper.

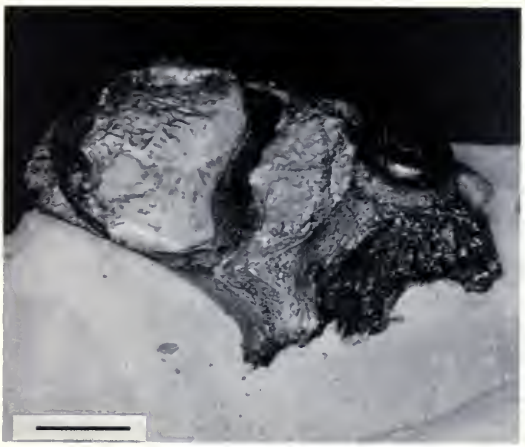


FIG. 15. ?*Cyamodus* sp. (MFSN 16848); partial palatine bone from Fus Creek, Moggio Udinese, Province of Udine, upper Ladinian. Scale bar = 10 mm.

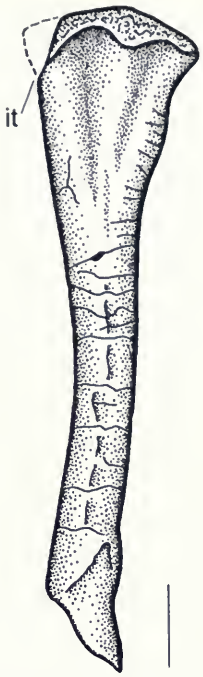


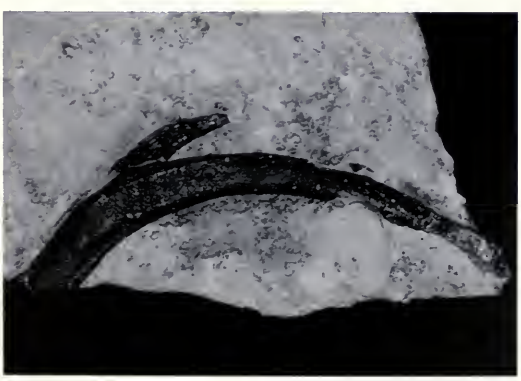
FIG. 17. *Nothosaurus* sp. (Museo Civico, Valdagno, uncatalogued); incomplete femur from Recoaro, Province of Vicenza, lower Anisian. Scale bar = 10 mm. Abbreviation: it, internal trochanter.

Nothosaurus sp.

MATERIAL—Museo Friulano di Storia Naturale, Udine, no. 19866; partial skull (Fig. 20).

LOCALITY AND HORIZON—Fusea near Tolmezzo, Province of Udine. "Black limestones" just above the "Dolomia Cassiana 2" (De Zanche et al., 1993), uppermost Julian, middle Carnian.

The specimen consists of the poorly preserved and strongly dorsoventrally compressed postorbital portion of a *Nothosaurus* skull, exposed in ventral view (Figs. 20, 21). As preserved, the total length of the specimen is 158.5 mm, the width across the mandibular condyles of the quadrates is 148.3 mm, and the width across the posterior ends of the squamosals is 81.5 mm. The anterior end of the specimen exposes parts of the dermal skull roof, in particular the frontal and the posteriorly pointed left postfrontal, in ventral view. The left postfrontal shows part of the intact posterodorsal margin of the orbit. More posteriorly, the pterygoids are exposed in ventral view. The left pterygoid still preserves the medial margin of the subtemporal fossa. The suture between the two pterygoids is barely visible in their posterior part. The posterior margins of the pterygoids are complete and separated by a distinct step from the



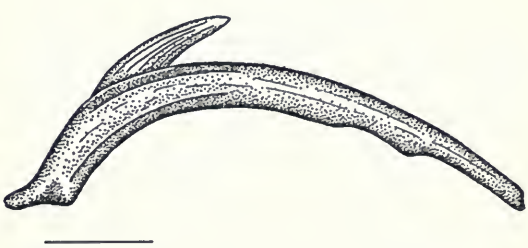


FIG. 16. *Nothosaurus* sp. (MFSN 15611); rib fragment with isolated tooth from Mt. Tersadia Massif, Arta Terme, Province of Udine, lowermost Anisian. Scale bar = 10 mm.

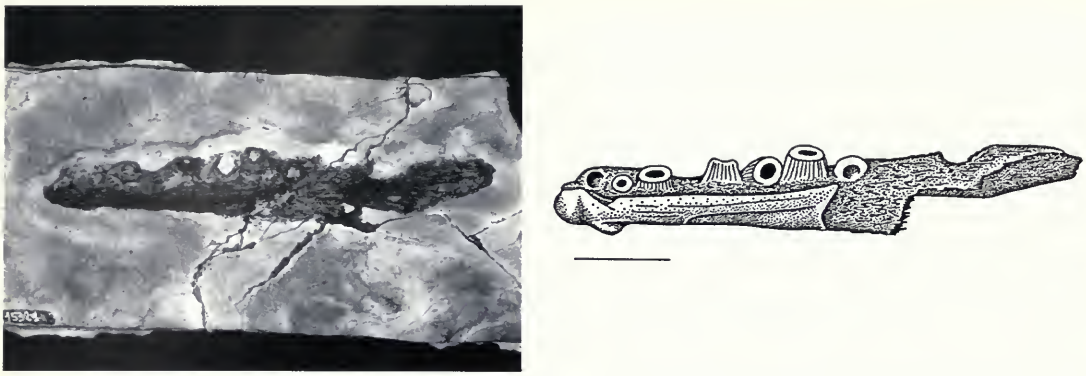


FIG. 18. *Nothosaurus* sp. (MFSN 15329); fragmentary mandible from Arta Terme, Mt. Tersadia, Province of Udine, upper Anisian. Scale bar = 20 mm.

overlying basioccipital. The occipital condyle is well preserved, as are the laterally oriented basioccipital tubera. The eustachian foramina are open on both sides of the basicranium. No further anatomical details of the occiput can be identified.

The medially and laterally descending flanges on the quadrate ramus of the pterygoid, from which the deep pterygoideus muscle originates, remain identifiable on both sides despite extensive crushing and dorsoventral compression of the skull. Due to extensive breakage, the suture joining the quadrate ramus of the pterygoid to the quadrate cannot be identified. The concave articular facet on the mandibular condyle of the quadrate is well exposed on the right side of the skull; its shape suggests a saddle-shaped articular facet on the lower jaw. On both sides of the skull, the posterior extremities of the upper temporal arches (squamosals) are preserved and exposed in ventral view.

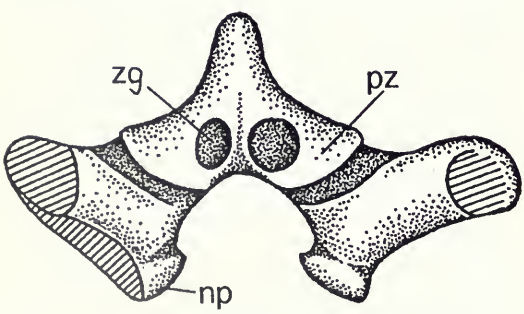


FIG. 19. *Nothosaurus* sp. (MFSN 21133); neural arch, Lavaz Creek, Dogna, Province of Udine, middle Carnian. Scale bar = 10 mm. Abbreviations: np, neural arch pedicel; pz, postzygapophysis; zg, zygantrum.

Most of the nothosaur remains from the Fusea locality can be referred to *Nothosaurus* cf. *N. giganteus* (see below). Specimen MFSN 19866 is too poorly preserved to be diagnostic at the species level. Its relatively smaller size makes it conceivable that it represents a different, smaller species (such as *Nothosaurus mirabilis*), but at the same time nothing precludes the possibility that it is merely a relatively small (immature) specimen of *Nothosaurus* cf. *N. giganteus.*

Nothosaurus cf. *N. giganteus* Münster, 1834

MATERIAL—Museo Friulano di Storia Naturale, Udine, no. 16849, sacral vertebra; nos. 16850, 16851, dorsal vertebrae; no. 17248, anterior dorsal neural arch; no. 17249, isolated centrum; no. 19288, partial skull; no. 22000, lower jaw fragment; no. 22004, lower jaw fragment with tooth; and no. 22916, distal end of left clavicle.

LOCALITY AND HORIZON—Fusea near Tolmezzo, Province of Udine. "Black limestones" just above the "Dolomia Cassiana 2" (De Zanche et al., 1993), uppermost Julian, middle Carnian.

Specimens 16849, 16850, and 16851 were previously described and illustrated by Dalla Vecchia (1993) and referred to "*Paranothosaurus.*" Rieppel and Wild (1996) have shown that *Paranothosaurus* Peyer, 1939, is a junior synonym of *Nothosaurus* Münster, 1834.

The partial skull MFSN 19288 closely resembles the specimen MFSN 19866 described above, except for its larger size (Fig. 22). The maximum length

FIG. 20. *Nothosaurus* sp. (MFSN 19866); partial skull in ventral view from Fusea near Tolmezzo, Province of Udine, middle Carnian. Scale bar = 50 mm.

of the skull fragment is 228 mm, and the distance from the mandibular condyle of the right quadrate to the ventral midline of the dermal palate (pterygoids) is 116 mm. Collected from the rock surface, the specimen is incomplete, strongly dorsoventrally compressed, and badly eroded. The skull is preserved in ventral view, exposing the anterior part of the skull roof (in internal view) and the posterior part of the basicranium. Details of the sutures can no longer be identified. Anteriorly, the ventral (internal) surface of the frontal shows two prominent, parallel and longitudinally oriented ridges, defining a trough that may have housed the tractus olfactorii. Anterolateral expansions of the skull roof probably represent the postfrontals. The left suspensorium is missing altogether, but fragments of the posterior part of the left upper temporal arch (squamosal) are preserved. The right suspensorium is crushed to an extent that sutural details can no longer be identified. However, its contours clearly indicate the posteriormost part of the right squamosal, as well as the (partially eroded) mandibular condyle of the right quadrate. The posterior margin of the pterygoids forms a distinct step in front of the occipital condyle.

MFSN 22000 represents a fragment of the lower jaw comprising the mandibular articulation (Fig.

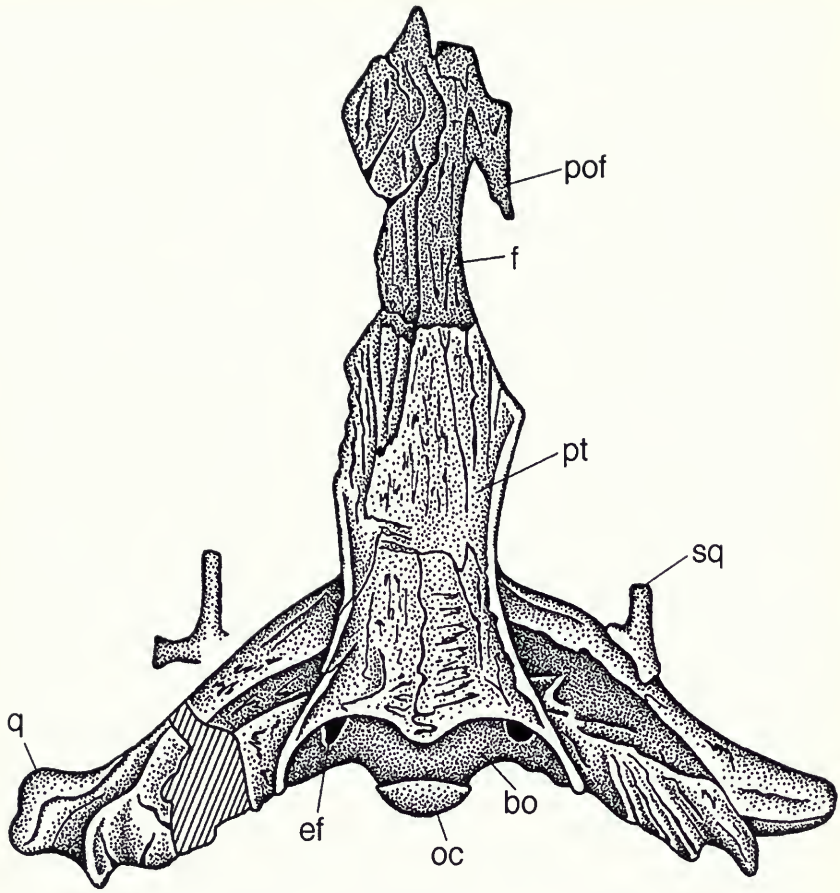


FIG. 21. *Nothosaurus* sp. (MFSN 19866); partial skull in ventral view from Fusea near Tolmezzo, Province of Udine, middle Carnian. Scale bar = 20 mm. Abbreviations: bo, basioccipital; ef, eustachian foramen; f, frontal; oc, occipital condyle; pof, postfrontal; pt, pterygoid; q, quadrate; sq, squamosal.

23A–B). As preserved, the specimen is 73.5 mm long. Although eroded, the ventromedial surface shows the medial expansion of the angular below the mandibular articulation, as is characteristic of *Nothosaurus* (Rieppel & Wild, 1996). The dorsolateral surface of the surangular forms a distinct horizontal shelf in front of the mandibular articulation for the insertion of fibers of the superficial jaw adductor muscle. The articular facet itself is deeply concave. MFSN 22004 represents another mandibular fragment of 65.6 mm length that shows a replacement tooth embedded in the (eroded) bone (Fig. 23C). The replacement tooth is near to full size, its exposed part measuring 27.5 mm in length, and it shows the distinctly striated enamel surface that is characteristic of *Nothosaurus*.

MFSN 17249 represents a strongly dorsoventrally compressed dorsal centrum with a maximum length of 34.0 mm and a maximum width of 43.3 mm. The dorsal view of the specimen rather nicely displays the "cruciform" or "butterfly-shaped" expansion of the sutural facets for the neural arch pedicels. The neural canal itself appears constricted at the middle of the centrum, symmetrically expanding toward the latter's anterior and posterior margins.

MFSN 17248 (Fig. 24A) represents an isolated anterior dorsal neural arch that is anteroposteriorly compressed and distorted. The posterior surface of the specimen is completely eroded. The total height of the neural arch is 39.4 mm, the width across the prezygapophyses is 43.8 mm, and the width across the transverse processes is

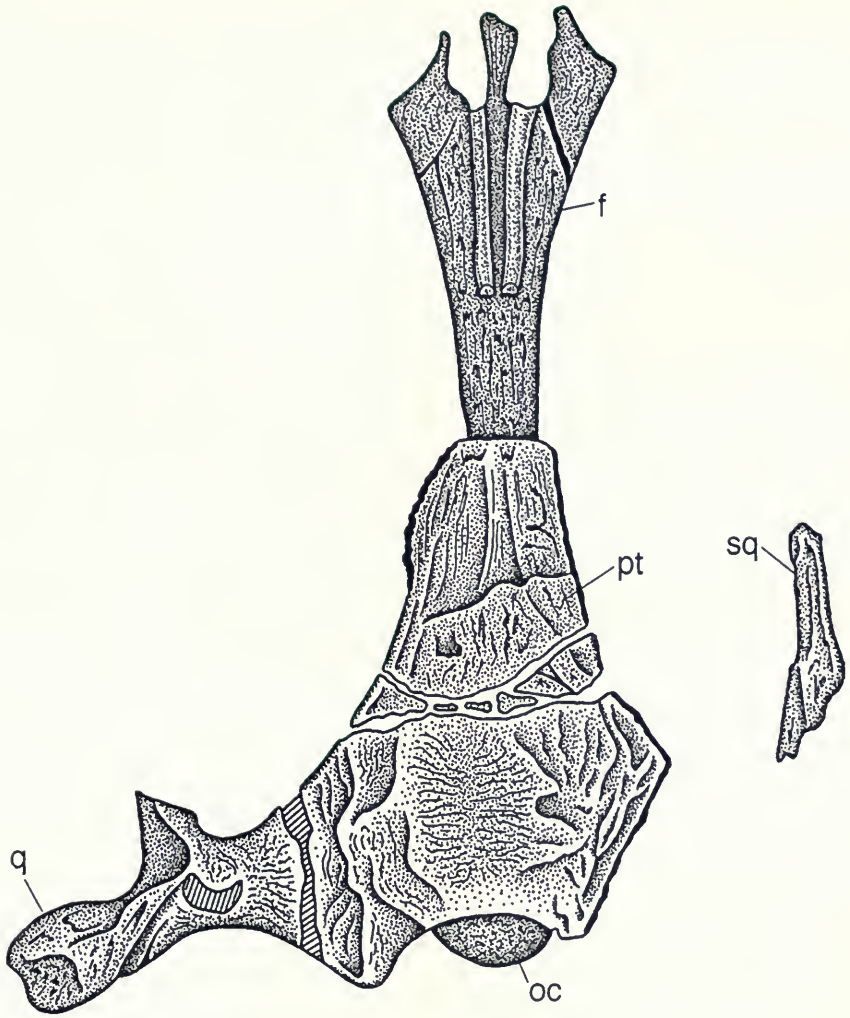


FIG. 22. *Nothosaurus* cf. *N. giganteus* (MFSN 19288); partial skull in ventral view from Fusea near Tolmezzo, Province of Udine, middle Carnian. Scale bar = 50 mm. Abbreviations: f, frontal; oc, occipital condyle; pt, pterygoid; q, quadrate; sq, squamosal.

47.9 mm. Distortion renders it difficult to judge the degree of dorsomedial inclination of the articular surfaces on the prezygapophyses, but they appear to be inclined to a lesser degree than the prezygapophyses in a more posterior dorsal vertebra (MFSN 16850, described below). The transverse processes extend along the entire height of the pedicels, as is characteristic of "*Paranothosaurus*" (Peyer, 1939). The transverse processes project laterally to a lesser degree in the anterior dorsal region than is the case in the middle and posterior dorsal region (specimen MFSN 16850, described below). The zygosphene is distinct on the anterior surface of specimen MFSN 17348, projecting from between the prezygapophyses. Although broken, the zygosphene retains a clear indication of its original bifurcation. The zygantrum can therefore be assumed to have been subdivided by a vertical septum.

MFSN 16850 (Fig. 24B) represents a middle or posterior dorsal vertebra. The neural arch is still in articulation with the centrum, but the neurocentral suture remains distinct. The total height of the specimen is 86.0 mm, the width across the

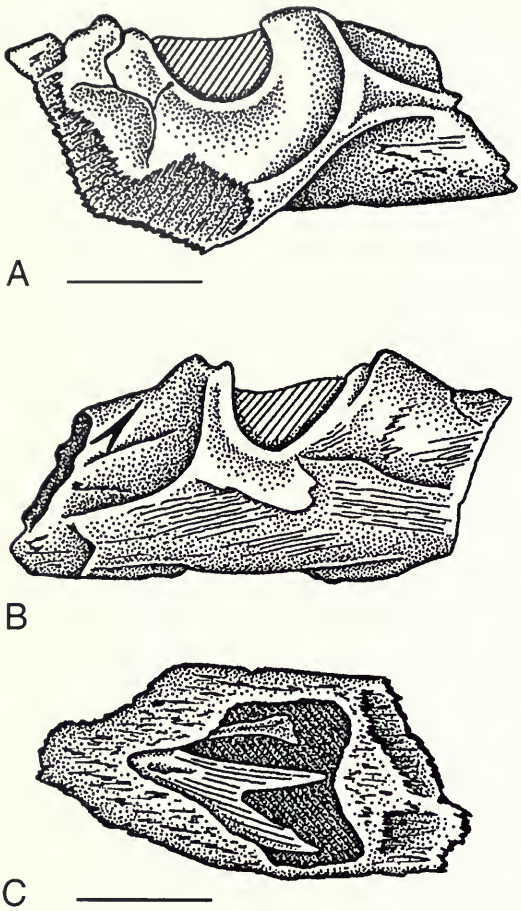


FIG. 23. *Nothosaurus* cf. *N. giganteus.* **A** and **B,** MFSN 22000; lower jaw fragment from Fusea near Tolmezzo, Province of Udine, middle Carnian. Scale bar = 20 mm. **C,** MFSN 22004; mandibular fragment with embedded replacement tooth from Fusea near Tolmezzo, Province of Udine, middle Carnian. Scale bar = 20 mm.

prezygapophyses is 46.5 mm, and the width across the transverse processes is 70.6 mm. The height of the neural spine, measured from the roof of the neural canal to its (complete) dorsal margin, is 42.3 mm. The vertical diameter of the neural canal is 8.2 mm and its horizontal diameter is 10.5 mm. The vertical diameter of the anterior articular surface is 36.5 mm and its horizontal diameter is 41.8 mm.

The vertebra is slightly compressed anteroposteriorly and distorted. The body of the centrum is distinctly constricted, and its articular surface is platycoelous. The centrum does not participate in the formation of the transverse processes. The transverse processes are deep and stout, and extend along the entire height of the pedicels of the neural arch. They extend laterally well beyond the prezygapophyses. The prezygapophyses are well preserved, their articular surfaces facing dorsomedially to a greater degree than is observed in the anterior dorsal neural arch described above (MFSN 17248) or in a sacral vertebra described below (MFSN 16849). The postzygapophyses are partially eroded; their articular facets face lateroventrally. The base of the eroded zygosphene is distinct at the base of the anterior margin of the neural spine between the prezygapophyses. The zygantrum forms a broad trough between the postzygapophyses and at its base retains vestiges of the vertical septum that subdivided it internally. The dorsal margin of the neural spine is complete, indicating a relatively low height.

MFSN 16849 is a posterior dorsal or sacral vertebra, again partially eroded and anterodorsally compressed (Fig. 24C). The total height of the element (as preserved) is 83.5 mm, the width across the prezygapophyses is 66.3 mm, the width across the postzygapophyses is 67.4 mm, and the maximal width across the transverse processes is 54.5 mm. The anterior articular surface has a vertical diameter of 33.5 mm and a horizontal diameter of 37.3 mm. The body of the centrum is constricted, and its articular surface is platycoelous. The dorsal margin of the neural spine is complete, indicating its relatively low height. The pre- and postzygapophyses are broad and dome-shaped, as is typical for "*Paranothosaurus.*" The articular facets on the pre- and postzygapophyses are almost horizontally oriented. Despite partial erosion, the zygosphene is still distinct, projecting from the base of the neural spine between the prezygapophyses and retaining some evidence of its bifurcated tip. The zygantrum again forms a wide trough between the postzygapophyses, retaining the dorsal part of the vertical septum that subdivided it internally.

The transverse processes do not extend laterally to a level beyond the pre- and postzygapophyses. They are high, formed by the pedicels of the neural arch with a participation from the centrum. The neurocentral suture remains distinct in the lower part of the transverse processes.

MFSN 22916 represents the distal end of a large left clavicle (Fig. 25). The element is dorsoventrally compressed and tapers to a blunt tip distally. Its size (the fragment is 163.5 mm long) is, again, indicative of a large species of *Nothosaurus,* as is the skull (MFSN 19288).

The vertebrae of *Nothosaurus* cf. *N. giganteus*

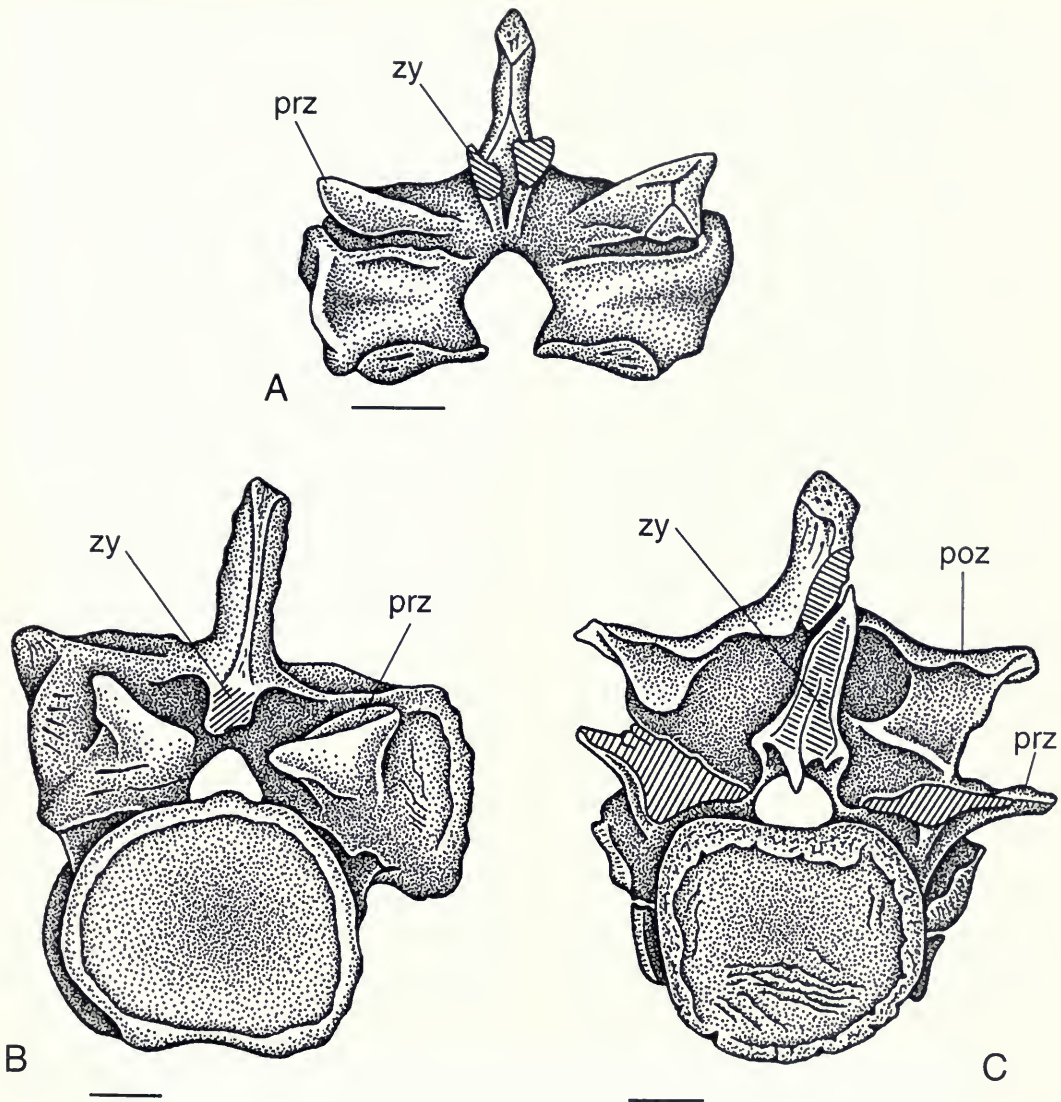


FIG. 24. *Nothosaurus* cf. *N. giganteus*. **A,** MFSN 17248, anterior dorsal neural arch from Fusea near Tolmezzo, Province of Udine, middle Carnian. **B,** MFSN 16850, middle or posterior dorsal vertebra from the same locality. **C,** MFSN 16849, posteriormost dorsal or sacral vertebra from the same locality. Scale bar = 20 mm. Abbreviations: poz, postzygapophysis; prz, prezygapophysis; zy, zygantrum.

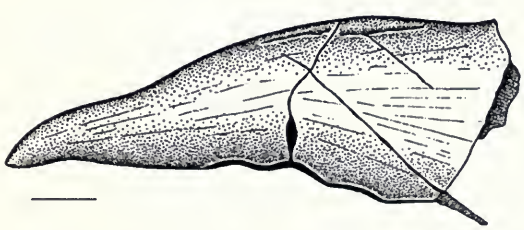


FIG. 25. *Nothosaurus* cf. *N. giganteus* (MFSN 22916); distal end of a left clavicle from Fusea near Tolmezzo, Province of Udine, middle Carnian. Scale bar = 20 mm.

from Fusea are important because they support the assessment of *Paranothosaurus* Peyer, 1939, as a subjective junior synonym of *Nothosaurus* Münster, 1834 (Rieppel & Wild, 1996). "*Paranothosaurus*" was distinguished from *Nothosaurus* not only by its larger size but also by the low neural spines on the dorsal vertebrae and by the stout transverse processes of the dorsal vertebrae extending over the entire height of the neural arch pedicels (Peyer, 1939). The diagnostic value of low neural spines was discussed by Kuhn-Schny-

der (1966), who indicated the possibility that the low neural spines in the holotype of *Paranothosaurus amsleri* could be an artifact from the dorsoventral compression of the specimen. Neural arches from the upper Muschelkalk of the Germanic Triassic that were not subject to compression indicate the presence of a large nothosaur with low neural spines in the dorsal vertebral column. These vertebrae were attributed to *Nothosaurus giganteus* Münster, 1834, by Rieppel and Wild (1996). This identification, in addition to the observation (Dalla Vecchia, 1993) that three dimensionally preserved vertebrae from Fusea indicate the presence of a large nothosaur with low neural spines in the Alpine Triassic, led to the conclusion that the genus *Paranothosaurus* Peyer, 1939, has to be treated as a subjective junior synonym of *Nothosaurus* (Rieppel & Wild, 1996). Whether the species *Paranothosaurus amsleri* Peyer, 1939, must also be treated as a subjective junior synonym of *Nothosaurus giganteus* Münster, 1834, or whether the large nothosaurs with the low neural spines in the Germanic and Alpine Triassic belong to different species, is a question that remains unresolved, largely because of the incompleteness of the available material.

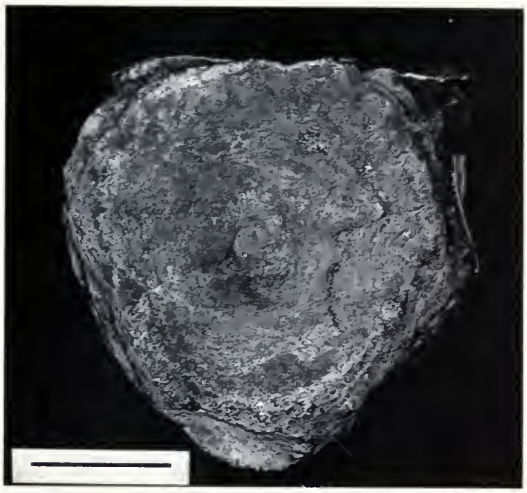


FIG. 26. *Cymbospondylus* sp. (MSNB 4949); dorsal vertebral centrum from Valzurio, Province of Bergamo, Anisian. Scale bar = 20 mm.

Discussion

The southeastern Alps of the Tre Venezie area in Italy have yielded sauropterygians from a variety of fossiliferous sites ranging in age from the earliest Anisian (Aegean) Lower Serla Dolomite and the early Anisian (Bithynian) *Gracilis* Zone of Recoaro to the middle Carnian. Exceedingly rare in the early Anisian of the Alpine Triassic, sauropterygians become more frequent in the late Anisian. This reflects the development of carbonate platforms with intraplatform basins along the southeastern shelf of the European platform during the Anisian (Marcoux et al., 1993). The first Mesozoic carbonate platform to develop in the Tre Venezie area is slightly older than the *Gracilis* Formation (the latest Spathian to Aegean Serla Dolomite). The richest fossiliferous locality is Fusea near Tolmezzo, which is of middle Carnian age. Sauropterygians from the middle Carnian might represent the geologically youngest occurrence of *Nothosaurus* in the Alpine Triassic (but see below).

It is interesting to note that the faunal composition of sauropterygians in the southeastern Alps of the Tre Venezie area differs radically from that observed in the southwestern Alps of southern Switzerland and the northern Italian Varese and Como Provinces. Fossiliferous localities in the latter area include the Monte San Giorgio, Cá del Frate, and Viggiù (uppermost Anisian and lower Ladinian: Kuhn-Schnyder, 1974), the Perledo, Esino, and Lecco localities with outcrops of the Perledo Member of the Perledo–Varenna Formation (upper Ladinian; Gaetani et al., 1992), and outcrops of the Kalkschieferzone (uppermost Ladinian) at Monte San Giorgio and Cà del Frate (Tintori & Renesto, 1990; Furrer, 1995). Collectively, these deposits have yielded abundant sauropterygian material from the Anisian–Ladinian boundary upward. However, the genus *Placodus* was never recorded in any of these localities, and the genus *Nothosaurus* remains very rare in these deposits and has never been recorded in middle or upper Ladinian deposits. Instead, the predominant sauropterygians of these deposits are pachypleurosaurs and lariosaurs (Rieppel, 1998b). Pachypleurosaurs extend up into the middle Ladinian, lariosaurs into the late Ladinian. This faunal composition contrasts with the faunas from the Tre Venezie area, where no pachypleurosaurs (other than a small vertebra from the *Gracilis* Formation of Recoaro: Rieppel & Hagdorn, 1997) and no lariosaurs are recorded. Instead, there are at least two occurrences of *Placodus,* and the most abundantly found sauropterygians represent at least two and probably three different species of *No-*

FIG. 27. *Lariosaurus calcagnii* (MSNB 8030); humerus from Val Rogno, Province of Bergamo, Carnian. Scale bar = 20 mm.

thosaurus. The only faunal component common to both areas is the cyamodontoid placodonts.

Rare and as yet undescribed sauropterygian remains from the Bergamo Province of northern Italy are housed in the Museo Civico di Scienze Naturali "E. Caffi" (MSNB), Bergamo. All of this material is Carnian in age, except for an anterior caudal vertebra of *Cymbospondylus* (MSNB 4949, with a diameter of approximately 57 mm; Fig. 26) from the Anisian of Valzurio. Cyamodontoid placodonts are represented by a dorsal vertebra from the Carnian of Monte Pora (MSNB 4755, original of Nosotti, 1987, Fig. 3). Eosauropterygians are represented by a beautifully preserved humerus of *Lariosaurus calcagnii* (MSNB 8030, Fig. 27) from the Carnian of Val Rogno, with a total length of 120.6 mm. The humerus has a strongly curved appearance, an evenly convex preaxial margin due to the reduction of the deltopectoral crest, and is not waisted in the mid-diaphyseal region as is typical for *Nothosaurus*. MSNB 4764 (Fig. 28) is a specimen from the Carnian of S. Gallo (Madonna della Costa) that may represent a smaller lariosaur or a large pachypleurosaur. Exposed are a slender and elongate femur, tibia, fibula, vertebrae, and rib fragments. The presence of pachypleurosaurs is further indicated by numerous small elements from various localities. A peculiar thoracic rib (MSNB 277, Fig. 29) also comes from the Carnian of S. Gallo (Madonna della Costa). This rib is characterized by a distinct proximal curvature and a distal portion that is distinctly broadened and flattened; with respect to this latter character it resembles very closely two isolated ribs with a similarly strong distal expansion from the upper Gipskeuper (Carnian) of Baden-Württemberg, southern Germany (Rieppel, 1996, Fig. 6). Although tentatively identified as ribs of a cyamodontoid placodont, the taxonomic affinity of these ribs is best left open for the time being, because

FIG. 28. *Sauropterygia* indet. (MSNB 4764); partial skeleton from S. Gallo (Madonna della Costa), Province of Bergamo, Carnian. Scale bar = 20 mm.

FIG. 29. *Sauropterygia* indet. (MSNB 277); thoracic rib from S. Gallo (Madonna della Costa), Province of Bergamo, Carnian. Scale bar = 20 mm.

in the most widely distributed cyamodontoid from the Upper Triassic (Norian) of Northern Italy, *Psephoderma,* the ribs are fully fused with the transverse processes of the dorsal vertebrae (Pinna & Nosotti, 1989). Although comparatively rare, the faunal composition of the Carnian sauropterygians from the Bergamo Province (with lariosaurs and pachypleurosaurs present but lacking any indication of the occurrence of *Nothosaurus*) differs from the faunal composition of sauropterygians from the Tre Venezie area, more closely resembling that of localities west to Bergamo.

With respect to the faunal composition of sauropterygians, the localities from the Tre Venezie area resemble those of the eastern Alpine Triassic more closely than those of the southwestern Alps (Bürgin et al., 1991, Table 4). Conversely, a small fauna from the northern Alpine Ladinian shows the pachypleurosaur–lariosaur assemblage otherwise typical for the southern Alps (Zapfe & König, 1980; Rieppel, 1995c). The reasons for these differences in faunal assemblages in the northern, southern, and eastern Alpine Triassic remain unclear at the present time. Perhaps the faunas from the southwestern Alps have close evolutionary and biogeographic ties to the fauna from the Anglo-Germanic Basin, whereas those of the eastern and southeastern Alps may have established themselves both earlier and independently. A faunal exchange of sauropterygians between the southwestern Alpine realm and the Anglo-Germanic Basin began with the opening of the Burgundian Gate in the late Anisian and lasted through the Ladinian (Rieppel & Hagdorn, 1997). The sauropterygians from the Tre Venezie area may have established themselves in the developing intraplatform basin facies along an eastern route. More research is required on the Sauropterygia from throughout the Alpine Triassic, however, in order to obtain a more refined picture of phylogenetic and historical biogeographic patterns.

Acknowledgments

We express our gratitude to Dr. Marco Avanzini, Geological Curator at the Museo Tridentino di Scienze Naturali (Trento), Dr. Giuseppe Muscio, Curator at the Museo Friulano di Storia Naturale, Dr. Anna Paganoni, Curator at the Museo Civico di Scienze Naturali "E. Caffi" (MSNB), Bergamo, and Prof. Paolo Mietto from the Dipartimento di Geologia, Paleontologia e Geofisica of the University of Padua, for access to their collections and advice on the stratigraphy of the fossiliferous localities. N. C. Fraser and H.-D. Sues read an earlier draft of this paper, providing much

appreciated comments and criticisms. This study was supported by National Science Foundation grant DEB-9419675 (to O.R.).

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